Ecological, evolutionary and social constraints on reproductive effort: a reassessment of biennial breeding by hoary marmots

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**Abstract**

Biennial breeding is a rare life-history strategy observed in animal species living in harsh, unproductive environments. This behavior is thought to occur in 10 of 14 species in the genus *Marmota*, making marmots useful model organisms for studying its ecological and evolutionary implications. Biennial breeding in marmots is frequently described as an obligate behavior which evolved as a mechanism to mitigate the energetic costs of reproduction (Evolved Constraint hypothesis). However, recent anecdotal evidence suggests that it is a facultative behavior controlled by annual variation in climate and food availability (Environmental Constraint hypothesis). Finally, in social animals like marmots, biennial breeding could result from reproductive competition between females within social groups (Social Constraint hypothesis). We evaluated these three hypotheses using mark-recapture data from an 8-year study of hoary marmot (*Marmota caligata*) population dynamics in the Yukon. Annual variation in breeding probability was modeled using multi-state mark-recapture models, while other reproductive life-history traits were modeled with generalized linear mixed models. Hoary marmots were neither obligate nor facultative biennial breeders, and breeding effort was insensitive to evolved, environmental, or social factors. However, newly mature females were significantly less likely to breed than older individuals. Annual breeding did not result in increased mortality. Average fecundity and female survival were correlated with winter climate, as indexed by the Pacific Decadal Oscillation. Hoary marmots are less conservative breeders than previously believed, and the evidence for biennial breeding throughout *Marmota*, and in other alpine animals, should be re-examined. Prediction of future population dynamics requires an accurate understanding of life history strategies, and of how life history traits allow animals to cope with changes in weather and other demographic influences.

**Introduction**

Animals living in harsh, unpredictable environments may require unusual life history strategies to maximize their fitness. Biennial breeding or reproductive skipping, is one such strategy, and is practiced by only a few groups of long-lived birds and mammals that live in polar and alpine habitats (Heezik et al. 1994, Chastel 1995, Blumstein and Armitage 1999, Dane 2002). This behavior is generally explained as a way of maximizing lifetime reproductive output when frequent reproduction is energetically costly and dangerous (Wasser and Barash 1983, Chastel 1995, Jouventin and Dobson 2002, Griffin et al. 2007). However, harsh environments can also be highly stochastic (Wingfield and Kitaysky 2002, Schwartz and Armitage 2004, Martin and Wiebe 2004). In such situations, a conservative life history strategy involving biennial breeding may be maladaptive, because animals that skip one reproductive opportunity may not live long enough to reproduce in the future (Benton et al. 1995).

The best documentation for biennial breeding behavior comes from long-lived seabird species with small clutch sizes (Heezik et al. 1994, Chastel 1995, Jouventin and Dobson 2002). For example, most albatross species can live for 40 years or more and lay only one egg at a time (Jouventin and Dobson 2002). Reproductive skipping in albatrosses is related to the physiological costs of breeding but it may be beneficial for these species because their life histories prioritize parental investment in a very limited number of young, and because their long lifespans allow them to make up missed breeding opportunities (Jouventin and Dobson 2002). However, it remains unclear why biennial breeding persists in species with short lifespans and variable fecundity.

Among mammals, biennial breeding is common in the genus *Marmota*. Of the fourteen extant marmot species, ten have been reported to skip one or more years when breeding (Blumstein and Armitage 1999). As with biennial - breeding birds, most marmot species live in arctic or alpine environments with harsh but variable weather. Marmots are also relatively long lived and philopatric, making them a convenient choice for long-term population-level studies of breeding behavior. Three alternative but not mutually exclusive hypotheses could explain biennial breeding in marmots: the Evolved Constraint hypothesis, the Ecological Constraint hypothesis, and the Social Constraint hypothesis.

The Evolved Constraint hypothesis, predicts that biennial breeding in marmots is a canalized evolved strategy for minimizing the costs of reproduction in a harsh environment. This hypothesis is difficult to test directly. However, it leads to the prediction that annual breeding should be extremely rare or absent, and that females who breed twice in a row should incur a heavy fitness cost (Weimerskirch et al. 1987), either through reduced survival or fecundity. Breeding female hoary and Olympic marmots spend more time foraging, stay active later in the fall, and weigh less at immergence than non-breeders, which suggests that there is a physiological cost of breeding for marmots (Barash 1980). However, the impact of this energetic loss on survival has not been determined.

Both Olympic and hoary marmots are considered biennial breeders, but annual breeding has been anecdotally observed in both species (Kyle et al. 2007, Griffin et al. 2007). This leads to the Ecological Constraint hypothesis, which predicts that biennial breeding in marmots may only occur when the environment is too unproductive or the animal’s condition is too poor to support more frequent reproduction. Based on this hypothesis, annual breeding may be a common occurrence, but previous breeding state should be correlated with the probability of breeding in the current year due to the physiological costs described in Barash (1980). The Ecological Constraint hypothesis also predicts that the probability of breeding should be a function of environmental conditions, such as winter climate. However, the effects of environment and breeding history could be additive or interactive.

Because marmots are social animals, biennial breeding may also be caused by competition between females (Social Constraint hypothesis). Dominant females suppress reproduction by subordinates in both alpine and yellow-bellied marmot social groups (Armitage and Schwartz 2000, Hackländer et al. 2003). In alpine marmots, this behavior leads to higher survival among the dominant female’s offspring, which benefit from the presence of non-breeding subordinate adults during hibernation (Arnold 1990). Most biennial breeding marmot species are thought to practice reproductive suppression, but suppression has been difficult to document in wild populations (Wasser and Barash 1983, Griffin et al. 2007). In this case, the average probability of breeding should decrease as the number of mature females per group increases (Blumstein and Armitage 1998). Reproductive suppression may also result in decreased breeding probability for younger females, especially in larger groups (Armitage and Schwartz 2000).

We studied the breeding patterns of hoary marmots (*Marmota caligata*) in the Yukon, Canada using multi-state mark-recapture models. Hoary marmots occur in high-latitude and alpine habitat with harsh, unpredictable weather, and their social groups exhibit highly variable social structure, which makes them a uniquely appropriate model for testing our three hypotheses (Patil et al. 2013, Kyle et al. 2007). Our objectives were to determine the probability of annual and biennial breeding, and to evaluate the relative support for the three hypotheses described above. We also quantified the survival cost associated with reproduction, and compared this cost with the influence of winter climate on survival. Finally, we examined sources of variation in average social group fecundity and litter size to determine whether the processes that governed breeding probability also influenced other reproductive life history traits.

**Methods**

Study species

Hoary marmots are highly social arctic and alpine herbivores that live near patches of exposed talus scattered throughout the mountains of western Canada (Barash et al. 1980). Unlike other alpine marmot species, hoary marmot family groups may exhibit both monogamous and polygynous mating strategies (Kyle et al. 2007). Although dominant females may suppress reproduction by subordinates or practice infanticide, multiple litters per family group, from multiple females, are common. Typically, family groups contain only one dominant male, who fathers all offspring. In our study site, extra-pair paternity was infrequent, and the timing of juvenile emergence suggests that most reproduction occurs prior to emergence from hibernacula in the spring (Kyle et al. 2007).

Study Site

This study was conducted on hoary marmots inhabiting a single 4 km2 valley in the southwest Yukon (61º12’N, 138º16’W; 1700-2100m). The valley is entirely above tree-line, and is characterized by a mix of wet and dry tundra interspersed with talus. Dominant plant species include *Dryas octopetala, Cassiope tetragona, Carex spp.*, and a variety of dwarf willow species (*Salix spp*.) Hoary marmots, collared pikas (*Ochotona collaris*), and arctic ground squirrels (*Urocitellus parryii*) are the dominant herbivores, although caribou and Dall sheep are also present.

### Capture methods

From May to August, 1999 to 2004, we live-captured, marked and released most marmots in the population, Live-traps of various sizes (Tomahawk Live Trap Company, Tomahawk, WI) were baited with human urine (Taulman 1989) and live vegetation from the adjacent alpine meadows (Hansen 1975; Holmes 1984). Juveniles were captured upon emergence from the natal burrow in early- to mid-July. At first capture, all marmots were marked in each ear using No. 3 monel tags (National Band and Tag, Newport, Kentucky) and a small piece of colored wire. A unique alphanumeric combination was dyed (Clairol Hydrience, #52 Black Pearl, Clairol Canada, Montreal, Quebec or Nyanzol-D American Colour and Chemical Corp., Charlotte, NC) into the fur above the tail to allow for individual identification at up to 200 m with binoculars. Colored wires were replaced annually, and faded dyed markings were reapplied as necessary at subsequent recaptures. Marmots were also resighted opportunistically by all field personnel throughout the summer, and their locations recorded according to a north-oriented grid marked at 50m intervals with wooden stakes.

### Social group assignment

Most individuals were assigned to a social group based on observations of spring emergence from a common hibernaculum. If animals were not observed at emergence, we assigned social groups based on observation of social interactions and home-range overlap (Kyle et al. 2007). Individual home ranges were estimated using location data for resighted and radio-tagged marmots, which were analyzed in program Ranges V (Kenward and Hodder 1996). In a subset of marmots with known social group affiliations, group members had >75% overlap in the 95% kernel estimate of home range (Worton 1989). We therefore used 75% as a cutoff for statistical social group assignments. These assignments were then verified based on social interactions between individuals. Juveniles were assigned to the social group of their putative mother, which was subsequently verified using genetic markers (Kyle et al. 2007). Only marmots that could be confidently assigned to a social group in our study area (i.e. non-transients) were included in our analyses.

Analyses

From an initial dataset of 217 marmots trapped between 1999 and 2004, we created a second, more limited dataset consisting only of female marmots two years old or older (76 individuals, 203 marmot-years). We excluded yearlings from this dataset because hoary marmots are not reproductively mature until age two, and generally do not reproduce until age three. In each year, we classified marmots as breeders or non-breeders based on two criteria: genetic parentage assignment and evidence of lactation during capture. Finally, we generated an encounter history for each animal in which the individual was considered present if sighted or captured at least once that year.

In 2007-2009, a subset of four social groups was trapped, representing approximately half the population of the valley. All measurements and marking techniques were identical to those used in the earlier census. We could not definitively assign all litters to parents or determine the breeding status of all females in 2007-2009, so these data were excluded from our CMR analyses. However, the number of litters, and the number of juveniles per litter (within a week of emergence), were counted for all four social groups trapped in 2007-2009. Hoary marmot females produce one litter per year (Barash 1975; Kyle et al. 2007), so we used the number of litters as an estimate of the number of breeding females in those years. Data from 2007-2009 were used to evaluate the ability of our CMR models to predict the number of breeding females in a given year, and were incorporated into models of fecundity and litter size.

### Multi-state CMR analysis framework

We analyzed the adult female mark-recapture dataset using multi-state models (Lebreton et al. 1992, Nichols et al. 1994). This involved constructing a set of candidate models to explain variation in three parameters: Apparent survival (S), detection probability (p), and a ‘movement’ parameter describing the probability of moving between a ‘Non-breeder’ state and a ‘Breeder’ state (ψ). Before analyzing the data, we conducted a goodness-of-fit (GOF) test using program U-CARE (Choquet et al. 2009). Because we did not detect significant lack of fit in a fully time- and group-dependent global model, we were able to use Akaike’s Information Criterion corrected for sample size (AICC) to compare models (Burnham and Anderson 2002). Based on previous analyses (Patil et al. 2013), p was modeled as a constant. The mean detection probability was 0.96 *±* 0.02 (SE).

Candidate model set

Probability of breeding

We selected the models in our candidate model set to represent alternative hypotheses about the effects of age, social structure, climate, and previous breeding state on the probability of an individual choosing to breed. Age effects were included because we expected that older, more experienced marmots would be more likely to attempt reproduction than those which had recently matured. Previous breeding state was constrained to affect only older (> three year) marmots, because two-year-olds generally do not breed. Only 2 two-year-olds reproduced during the course of the study, and these individuals were excluded to simplify analyses.

We used the mean value of the Pacific Decadal Oscillation index (PDO) from November and May to model winter climate (<http://www.esrl.noaa.gov/psd/data/climateindices>). PDO is a 20-30 year cyclic pattern of climate variation in the North Pacific Ocean that correlates well with temperature and precipitation throughout northwestern North America (Mantua and Hare 2002; Mantuaet al. 1997). Within its multidecadal cycle, PDO also fluctuates annually. These annual fluctuations were negatively correlated with the date of spring snowmelt in an earlier study at our site (Morrison and Hik 2007), annual snow accumulation on nearby Mt. Logan (~100 km; Moore et al. 2002), and mean winter snow depth at two weather stations (Burwash Landing and Aishihik Lake) each located ~30km away from our study site but 1400m lower in elevation (r = 0.61 and 0.6 respectively for 1967-2007; Environment Canada http://www.climate.weatheroffice.ec.gc.ca/). Positive winter PDO values are therefore associated with early snowmelt and shallow snowpack, while negative values are associated with the opposite patterns.

The social environment was measured as i) the total number of non-juvenile marmots within the social group that were resighted or captured after July 1 during the previous summer and ii) the number of reproductively mature females in the group. Both covariates should be negatively correlated with breeding probability if reproductive suppression is a common occurrence. A complete list of covariates used, as well as their abbreviations, is given in Table 1.

Apparent survival

Survival models included only three covariates: winter PDO, winter PDO lagged by one year, and current breeding state. Previous survival analyses suggested that winter climate was by far the dominant influence on survival; however, those analyses did not include breeding state. We therefore chose this simplified model set in order to test the cost-of-reproduction hypothesis while accounting for the influence of climate on survival. The two PDO indices were not correlated (r=0.13, p=0.85).

CMR analyses / evaluation of fit

We constructed all mark-recapture analyses using program MARK and the RMark package in R (Laake and Rexstad 2007, R Development Core Team 2011). We ranked models using AICC (Akaike et al. 1973), and evaluated the relative importance of covariates by summing their AICC weights across the entire model set (Burnham and Anderson 2002). We also model-averaged Ψ and S across the entire model set (Burnham and Anderson 2002, Anderson 2008). Finally, we used the averaged Ψ values to predict the number of breeding females in 2007-2009. These predictions were compared with the estimated number of breeders from those years to test the generality of our results.

Fecundity models

We used generalized linear mixed models (GLMM’s) to examine the effects of winter PDO, lagged winter PDO, group size, and group\*climate interactions on three measures of hoary marmot fecundity. Models were fit using the lme4 package in R (Bates et al. 2012). The three response variables were juveniles per social group (n = 78), average fecundity (juveniles per adult female w/in group; n=66), and litter size using a dataset of all fully enumerated litters with known mothers identified by genetic analyses (n = 41; Kyle et al. 2007). Error distributions were chosen after testing for conformity to a Poisson distribution (Scrucca 2004). Random effects were included based on likelihood ratio tests using the most parameterized fixed-effects model in each model set (Bolker et al. 2009). Results of overdispersion tests, the error distributions and the random effects used for each response variable are shown in Table 2. In all cases, we ranked models and calculated the relative support for individual variables using AICC. Beta-coefficients were model-averaged, and unconditional standard errors for those coefficients were estimated by bootstrapping with 10,000 replications. The covariates used in all models are listed in Table 1.

**Results**

Breeding probability

The top model did not include previous breeding state as a covariate, but models with previous breeding state as a predictor of Ψ (the probability of moving into the ‘Breeder’ state) had a combined AIC weight of 0.48, and 3 models containing this covariate were within 2 AICc of the top model. Model selection therefore provided a moderate degree of support for effects of previous breeding state on current breeding effort (Table 3). However, the model-averaged effect size (difference in Ψ probability between breeders and non-breeders from the previous year) was < 0.01 (Fig. 1). Model selection did not support PDO as a predictor of Ψ (Table 4). Social group size had a combined AIC weight of 0.28 (Table 4), but the Group covariate was only present in one model within 2 AICc of the top model. The best model did not include annual variation in breeding probability (Table 3), and model-averaged Ψ estimates varied by less than 1 SE from year to year in both age-classes (Fig. 1).

Age-class had the strongest support of any model covariates, and had the largest effect size (Table 4; Fig. 1). Annual variation in Ψ was more pronounced for females in their first year of reproductive maturity, but the uncertainty in parameter estimates was also greater for this age-class (Fig. 1). On average, the breeding probability of females four years old or older was 0.33 greater than that of three-year-old individuals (Fig. 1).

When model-averaged parameters were used to predict the number of breeding females in a subset of the population during 2007-2009, the results were within 1-2 litters of the observed values in each year (Table 5). Year-to-year variation in the number of breeding females was also predicted accurately (Table 5).

Survival / cost of reproduction

Breeding state had a summed AIC weight of 0.33 as a predictor of survival, but its effect size (difference in apparent survival probability) was less than 0.01 (Table 4; Fig. 2). In contrast, PDO and PDO lagged by one year were predictors of survival in all supported models (Table 3). PDO and PDOlag were negatively correlated with survival, which declined over the course of the study by ~0.35 (Fig. 2).

The body condition index (log (mass/zygomatic arch length)) of non-breeding females increased faster over the course of the summer than that of breeders (Fig. 3). The difference in slopes was highly significant (Δ = 0.0021, p < 0.001, adjusted R2 = 0.60). On average, non-breeders had a greater body condition at the end of August than breeders (Fig. 3).

Group fecundity

The juveniles per group dataset contained significant Poisson overdispersion, so negative binomial models were used (Table 2). Likelihood-ratio tests did not support either slope or intercept random effects (Table 2). Social group size had a summed AIC weight of 0.86, which means that model selection strongly favored social group size as a predictor of the number of juveniles produced per group (Table 6). Each additional group member corresponded to ~1 additional juvenile (e 0.06 = 1.06; Table 7). There was also support for a relationship between juveniles per group and winter PDO. PDO had a summed AIC weight of 0.5, and PDOlag had a summed weight of 0.42. PDO was negatively correlated with the number of juveniles produced per group (Table 7). The bootstrap 95 % confidence interval for the PDO beta coefficient was large and overlapping with 0, but this overlap was less than 2% of the confidence interval width (Table 7). The model-averaged effect of PDOlag on juveniles per group was positive, but the 95% confidence interval for that coefficient overlapped with 0.

Juveniles per female (average fecundity)

AIC weights strongly supported a negative relationship between average fecundity and winter PDO (summed AIC weight = 0.97), and a positive relationship with PDOlag (Table 7). However, the 95 % confidence interval for the model-averaged PDO and PDOlag beta coefficients overlapped with zero. Social Group effects had a summed AIC weight = 0.47, but did not show a consistent negative or positive relationship with fecundity (Table 7). Interactions between climate and social effects were not as well supported as either main effect, and the confidence intervals for their beta coefficients all included positive and negative values. Likelihood ratio tests indicated significant random effects of social group (intercept effect) on average fecundity, but no random slope effects were supported (see Table 2).

Litter size

The null model had the smallest AICC value in the litter size model set, which means that litter size was not well predicted by group size, winter climate, or a combination of the two. The probability of a type II error was low. For example, for a model with litter size as a function of PDO alone, power associated with an effect size (Cohen’s f2) of 0.33, which corresponds to an R2 of 0.25 (Cohen 1988), was 0.95. Litter size ranged from one to six individuals, although these extreme values were rare. The mean litter size was three. Average litter size did not vary significantly between social groups (F9,41 = 0.61, p = 0.78).

**Discussion**

Hoary marmots are not obligate biennial breeders. Although a mature female marmot’s probability of breeding was close to 50% on average, none of the three hypotheses we examined (Evolved Constraints, Ecological Constraints, and Social Constraints) could adequately explain variation in breeding probability.

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Evolved Constraints

Contrary to the predictions of the Evolved Constraint hypothesis, breeding in the previous year had almost no effect on the probability that an individual would breed in the current year. This resultcontrasts with previous studies of hoary marmot breeding patterns (Barash 1974, Wasser and Barash 1983, Holmes 1984) in which biennial breeding was first suggested. However, the hypothesis of biennial breeding in hoary marmots was derived primarily from observation of behavioral associations between adult female marmots, yearlings, and juveniles, and not from data on the breeding success of individuals (Barash 1974).

Although our conclusions are different, our results concur with earlier studies of hoary marmot population dynamics in that approximately half of all mature females attempted to breed in any given year (Fig. 1). The fact that we were able to accurately predict the number of litters produced in 2007-2009 using models that were parameterized with data from 1999-2004 suggests that average breeding probability is relatively consistent over time, even though environmental conditions,social group composition, and the previous breeding states of individuals are not (Table 5). Although hoary marmots do not appear to have evolved to be obligate biennial breeders, our data lead us to hypothesize that their reproductive success may still be influenced by evolved physiological constraints. Further investigation into variation in marmot breeding patterns at larger spatial and temporal scales could help to reveal the full extent of this consistency in breeding effort, as well as the mechanisms behind it.

Ecological Constraints

Breeding probability was not sensitive to the depth and duration of snowpack the previous winter or to the length of the previous growing seasonas indexed by the winter PDO. Constant breeding probability could have evolved as a life history tradeoff to compensate for environmentally-driven variation in annual survival. Finally, a constant breeding effort may come at the expense of fecundity. This last hypothesis is consistent with our findings that average fecundity and juveniles per group declined during winters with thin snowpack (high PDO values) while breeding effort did not.

Social Constraints

Our results did not support the Social Constraint hypothesis. Had partial reproductive suppression of non-dominant females occurred, the average number of juveniles per female should have been negatively correlated with group size and the number of adult females per group (Blumstein and Armitage 1999). Instead, group size had almost no influence on breeding probability. Social group size also had little influence on average fecundity, and was positively related to the number of juveniles born per group in a given year. When social structure was modeled using the number of adult females as a covariate instead of total group size, the results were essentially the same.

Age affects breeding success in most mammal species (Harvey and Zammuto 1985), so it is not surprising that age-class was an important variable in our models of breeding probability. However, the biological significance of this result is ambiguous. A positive relationship between age and breeding success could be the result of partial reproductive suppression if older females were more likely to be dominant, as is the case in alpine marmots (Hackländer et al. 2003). On the other hand, social mechanisms are not required to explain a link between age and reproduction: younger females could simply be less effective at caring for their young, or less likely to reach parturition successfully. Because mating, birth, and weaning took place primarily underground at our site (Kyle et al. 2007), we cannot conclusively determine which explanation is correct.

Cost of reproduction

The seasonal activity patterns of breeding adult females in our study were consistent with those described by Barash (1980), and breeders were at an energetic disadvantage by the end of the season (Fig. 3). However, this difference had no measurable impact on apparent survival probabilities, implying that marmots were able to cope with the physiological stress of breeding. The energetic costs of breeding appear relatively unimportant for survival when compared to the effects of variable winter climate and snowpack, which appear to exert a strong influence on the conditions experienced by hoary marmots during hibernation (Patil et al. 2013). Our survival analyses are consistent with our breeding probability results, because without a high fitness cost of annual reproduction, it is not obvious what the selective pressure for biennial breeding might be.

Because our study site was near the northern extent of the hoary marmot's range, breeding females in our study had to cope with exceptionally harsh winters and a relatively short growing season during which to recoup their energetic losses (Patil et al. 2013), it seems seems unlikely that other populations of hoary marmots, most of which occur in milder climates, would have experienced greater mortality costs associated with breeding. Unfortunately, although the large latitudinal gradient encompassed by the hoary marmot's range makes them an ideal model for studying the effects of spatial variation in climate on costs of reproduction and other life history tradeoffs, there is virtually no demographic data available to support such analyses.

Comparisons with other marmot species

Despite its potential importance, variation in breeding probability has received less attention than fecundity or survival in demographic studies of mammals (Ozgul et al. 2007). A rough comparison has been made across the genus *Marmota*, and marmot species are remarkably similar in their average breeding probability (Bryant 2005). This consistency provides additional support for the notion of an intrinsic constraint on reproductive success that is unrelated to social pressures or environment. However, breeding success is influenced by winter weather in yellow-bellied marmots, and potentially in Olympic marmots as well (Schwartz and Armitage 2004, Griffin et al. 2007). In addition, the marmot species with the lowest reported rate of breeding success, the golden marmot (*Marmota caudata*), lives in an environment that is more arid, less productive, and at higher elevation than almost any other marmot species (Blumstein and Arnold 1998). For alpine marmots, winter weather does not affect breeding success, but body condition at the end of hibernation is important (Hackländer and Arnold 1999). Taken together, these studies support the Ecological Constraint hypothesis as an explanation for differences in breeding probability among marmot species.

It is not clear why intraspecific variation in hoary marmot breeding probability was less sensitive to climate than for other marmot species. Spatial variation in habitat quality can affect reproduction (Ozgul et al. 2007), so differences between social group territories could have obscured some underlying climate-related pattern. However, in a food addition experiment at our study site, marmots fed rabbit chow *ad libidum* did not show significant differences in mass accumulation rates, fall body mass, or overwinter survival compared to control animals (T.J. Karels et al. unpublished data). It is therefore conceivable that hoary marmots have also evolved breeding patterns that are insensitive to the timing and abundance of food availability.

The apparent absence of social constraints on hoary marmot reproduction was also an anomaly among marmot species. In *Marmota* and other ground-dwelling Sciurids, social complexity and breeding probability are generally negatively correlated (Armitage and Schwartz 2000, Blumstein and Armitage 1998). This pattern is most evident in alpine marmots, the most socially complex member of the genus. In alpine marmot social groups, only one dominant female is allowed to breed (Arnold 1990, Hackländer et al. 2003). However, even the dominant female’s reproductive output is reduced in large social groups, apparently due to reproductive competition with subordinates (Hackländer et al. 2003). Reproductive suppression has also been documented in yellow-bellied marmot groups, where the relationship between matriline size and reproductive rate is unimodal (Armitage and Schwartz 2000).

Hoary marmot breeding probability may be less constrained by group size because females within a group are closely related. In alpine marmots, the dominant female is less likely to breed when subordinates are unrelated, but not when subordinates are her siblings (Hackländer et al. 2003). Although genetic relatedness has not been comprehensively determined in our population, females rarely disperse from their natal group, and extra-pair copulation is almost non-existent (Kyle et al. 2007), so females within a social group are mostly offspring, grand-offspring, or siblings of each other. In addition, the number of adult females per social group is highly variable from one year to the next (Kyle et al. 2007), so the social dominance structure must also be unstable. Given these circumstances, all females in a social group may receive enough direct and indirect fitness benefits that reproductive competition is unnecessary.

Another potential explanation comes from life history theory, which predicts that life history parameters with the greatest potential influence on population dynamics should be the least variable (Ozgul et al. 2007). Hoary marmots may therefore have evolved a consistent probability of breeding because breeding probability is more important, demographically, than other aspects of their life history.

Breeding at a consistent rate every year may confer a long-term selective advantage on hoary marmots, but it may also result in maternal stress effects being passed on to juveniles (Sheriff et al. 2009). We cannot test this hypothesis directly, but juvenile hoary marmot survival is correlated with winter climate lagged by one year, which implies the operation of maternal effects (Patil et al. 2013). Ultimately, it may be impossible to pinpoint exactly how hoary marmot breeding patterns evolved, because a stochastic environment can select for more than one optimum life history strategy (Orzack and Tuljapurkar 2001).

**Conclusions**

There has been speculation that marmots are able to compensate for the negative effects of hibernation under a shallow snowpack by increasing their reproductive output during the resulting longer, more productive growing seasons (Griffin et al. 2007). We did not find evidence for this hypothesis, although climate-driven life history tradeoffs may be more important for marmots in less severe alpine environments than the Yukon (Griffin et al. 2007). In addition, our findings show that small, newly formed social groups containing younger females have lower reproductive output, and are therefore at greater risk of extinction than older groups with more experienced breeders. Demographic mechanisms of Allee effects have also been identified in yellow-bellied and alpine marmot populations (Armitage and Schwartz 2000, Stephens et al. 2002), and should be considered whenever effects of climate change on social animals are being studied.

Hoary marmots are less conservative in their breeding habits than previously believed. More generally, obligate biennial breeding is probably less common in *Marmota*, and in arctic/alpine fauna, than previous research suggests (see Griffin et al. 2007). Accurate characterizations of species' life histories are essential for understanding how climate change and other factors can influence population dynamics, and for predicting future population trends (Winkler and Dunn 2002, Jiguet et al. 2007). The evidence for biennial breeding and other unusual life-histories traits should therefore be re-examined.

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Table 1. Abbreviations and descriptions of covariates used in analyses of female hoary marmot reproductive parameters.

|  |  |
| --- | --- |
| **Abbreviation** | **Definition and Description** |
| PDO | Mean Pacific Decadal Oscillation from November to May during the most recent winter |
| PDOlag | Mean Pacific Decadal Oscillation from November to May during the previous year |
| Age | Two age classes: Young (3 years old), and Old (>3 years) |
| Mother Age | Minimum age of mother in years, for litter size analysis only |
| Group | Total number of non-juvenile marmots within social group |
| Ad. fems | Number of reproductively mature adult females in a social group |
| Time | Random annual variation |
| Brd. State | Factor variable. 1 = females that bred during the previous year, 0 = non-breeders in previous year |
| 1 | No time variation (constant) |
| Young | Denotes a linear covariate applied only to female marmots 3 years of age. |
| Old | Covariates applied only to female marmots >3 years old. |
|  |  |

Table 2. Results of Poisson overdispersion tests (Scrucca 2004) for three measures of hoary marmot fecundity, based on data from 10 hoary marmot social groups in the Ruby Range, Yukon Territory, 1999-2004 and 2007-2009. The corresponding linear model types used to model those variables are also shown. Error distributions were chosen based on test results. If significant overdispersion was present, negative binomial generalized linear models were used. If Poisson underdispersion was detected, Gaussian errors were used. Random effects (Social Group affiliation, and interaction between Social Group interaction and fixed effect slopes) were included based on likelihood-ratio tests using the most parameterized fixed-effect model in each model set (Bolker et al. 2009).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response Variable** | **Obs./Theor.Var** | **Statistic** | **p** | **Error Distribution** | **Random Effects** |
| Juveniles/Group | 3.83 | 248.64 | 0.00 | Neg. Binomial | None |
| Juveniles/Female | 1.29 | 84.14 | 0.06 | Poisson | Social Group,  Social Group\*PDO |
| Known Litter Size | 0.57 | 23.33 | 0.99 | Gaussian | None |

Table 3. Model-selection results for multistate CMR analyses of adult female hoary marmot survival and breeding probability in the Ruby Range, Yukon Territory from 1999-2004. Parameters shown are survival probability (S), and the probability of breeding in a given year (Ψ). Detection probability (p) was modeled as a constant, and was estimated at 0.96 ± .02 (SE). Descriptions and abbreviations for all covariates are in Table 1. K is the number of estimated model parameters and ωis the model’s AIC weight.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **K** | **AICC** | **∆ AICc** | **ω** |  |
| **S** PDO + PDOlag **Ψ** Age | 6 | 384.19 | 0 | 0.29 |  |
| **S** PDO + PDOlag **Ψ** Old: (Brd. State + Group)  Young: Group | 8 | 385.28 | 1.09 | 0.17 |  |
| **S** PDO + PDOlag  **Ψ** Old: Brd. State  Young: 1 | 7 | 385.73 | 1.55 | 0.14 |  |
| **S** PDO + PDOlag + Brd. State **Ψ** Age | 7 | 385.93 | 1.75 | 0.12 |  |
| **S** PDO + PDOlag + Brd. State **Ψ** Old: Brd. State + Group  Young: Group | 9 | 387.09 | 2.9 | 0.07 |  |
| **S** PDO + PDOlag + Brd. State **Ψ** Old: Brd. State  Young: 1 | 8 | 387.51 | 3.33 | 0.06 |  |
| **S** PDO + PDOlag **Ψ** Old: Ad. Fems  Young: 1 | 6 | 387.91 | 3.73 | 0.05 |  |
| **S** (PDO + PDOlag ) \* Brd. State **Ψ** Age | 9 | 388.71 | 4.53 | 0.03 |  |
| **S** PDO + PDOlag + Brd. State **Ψ** Old: Ad. Fems  Young: 1 | 7 | 389.66 | 5.47 | 0.02 |  |
| **S** PDO + PDOlag **Ψ** Old: Group  Young: 1 | 6 | 389.85 | 5.66 | 0.02 |  |
| **S** (PDO + PDOlag ) \* Brd. State **Ψ** Old: (Brd. State + Group) Young: Group | 11 | 389.97 | 5.79 | 0.02 |  |
| **S** (PDO + PDOlag ) \* Brd. State **Ψ** Old: Brd. State  Young: 1 | 10 | 390.36 | 6.17 | 0.01 |  |
| **S** PDO + PDOlag  **Ψ** Old: Brd. State + PDO + PDOlag + Group  Young: PDO + PDOlag + Group | 12 | 390.75 | 6.57 | 0.01 |  |

Table 4. AIC weights (ω**+**) for all covariates summed across all candidate models in a multi-state CMR analysis of adult female hoary marmots in the Ruby Range, Yukon, 1999-2004. Covariates of both survival (S) and breeding probability (ψ) are shown. Covariate descriptions are in Table 1. '\*' indicates an interaction term between two main effects.

|  |  |
| --- | --- |
| **Covariate** | **ω+** |
| **Ѱ** |  |
| Age | 1 |
| Brd. State | 0.47 |
| Age\*Brd. State | 0.47 |
| Group | 0.28 |
| Age\*Group | 0.28 |
| Ad. Fems | 0.06 |
| PDO | 0.01 |
| PDOlag | 0.01 |
| Age\*PDO | 0.01 |
| Age\*PDOlag | 0.01 |
| Age\*Ad. Fems | 0 |
|  |  |
| **S** |  |
| PDO | 1 |
| PDOlag | 1 |
| Brd. State | 0.33 |
| Brd. State\*PDO,PDOlag | 0.06 |

Table 5: Observed and predicted number of breeding females summed across four hoary marmot social groups from the Ruby Range, Yukon, 2007-2009. Predictions were based on model-averaged breeding probability estimates derived from the same study site in 1999-2004, assuming one litter per breeding female per season. Predictions were rounded to the nearest whole number.

|  |  |  |
| --- | --- | --- |
|  | **Predicted** | **Observed** |
| 2007 | 6 | 7 |
| 2008 | 8 | 10 |
| 2009 | 3 | 4 |

Table 6. Model-selection results for linear models of hoary marmot reproductive parameters. K is the number of estimated model parameters and ω is the AIC weight. Response variables were the number of juvenile produce per social group and average fecundity (juveniles per female within social group). Data were collected 1999-2004 and 2007-2009 from 10 social groups in the Ruby Range, Yukon Territory. The error distribution used and the type of model are shown in italics below the name of each response variable. GLMM’s are Generalized Linear Mixed Models, and GLM’s are Generalized Linear Models. Only models with ∆ AICC < 7 are shown.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Model** | **K** | **AICC** | **∆ AICC** | **ω** |
| Juveniles Per Group |  |  |  |  |
| (*Negative Binomial GLM's*) |  |  |  |  |
| Group | 3 | 315.63 | 0 | 0.22 |
| Group+PDO | 4 | 315.88 | 0.25 | 0.19 |
| Group+PDOlag | 4 | 316.12 | 0.48 | 0.17 |
| Group+PDO+PDOlag | 5 | 316.55 | 0.92 | 0.14 |
| Group\*PDO | 5 | 317.91 | 2.28 | 0.07 |
| Null | 2 | 318.33 | 2.69 | 0.06 |
| PDO | 3 | 318.35 | 2.71 | 0.06 |
| Group\*PDOlag | 5 | 318.46 | 2.82 | 0.05 |
| PDOlag | 3 | 320.45 | 4.82 | 0.02 |
| PDO+PDOlag | 4 | 320.56 | 4.93 | 0.02 |
| Group\*(PDO+PDOlag) | 7 | 320.87 | 5.24 | 0.02 |
|  |  |  |  |  |
| Juveniles Per Female |  |  |  |  |
| (*Poisson GLMM's*) |  |  |  |  |
| PDO+PDOlag | 4 | 185.04 | 0 | 0.38 |
| Group\*(PDO+PDOlag) | 7 | 186.98 | 1.94 | 0.14 |
| Group+PDO+PDOlag | 5 | 187.23 | 2.19 | 0.13 |
| Group\*PDO | 5 | 187.32 | 2.28 | 0.12 |
| PDO | 3 | 187.66 | 2.62 | 0.1 |
| Group+PDO | 4 | 188.34 | 3.3 | 0.07 |
| PDOlag | 3 | 189.87 | 4.83 | 0.03 |

Table 7. Model-averaged beta coefficients (β) , bootstrapped unconditional standard errors (SE), 95% confidence interval lower and upper limits (LCL and UCL), and summed AIC weights (ω+) of parameters for models of group fecundity, individual fecundity (juveniles/adult female), and litter size of hoary marmots in the Ruby Range, Yukon Territory. SEs and 95% confidence limits were bootstrapped with 1000 replications. Except for litter size, analyses were based on data from 1999-2004 and 2007-2009. Due to highly significant poisson overdispersion, juveniles per group were modeled using negative binomial linear models. Juveniles per female were modeled using Poisson mixed models with social group random effects. Litter size data were approximately normally distributed, and were modeled as such.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **Model-averaged β** | **SE** | **LCL** | **UCL** | **ω+** |
| Juveniles Per Group |  |  |  |  |  |
| (*Negative Binomial GLM's*) |  |  |  |  |  |
| PDO | -0.13 | 0.36 | -1.24 | 0.03 | 0.73 |
| PDOlag | 0.09 | 0.19 | -0.17 | 0.58 | 0.41 |
| Group | 0.06 | 0.04 | 0.00 | 0.14 | 0.85 |
| Group\*PDO | 0.00 | 0.03 | -0.02 | 0.12 | 0.08 |
| Group\*PDOlag | 0.00 | 0.02 | -0.02 | 0.05 | 0.07 |
|  |  |  |  |  |  |
| Juveniles per female |  |  |  |  |  |
| (*Poisson GLM's*) |  |  |  |  |  |
| PDO | -0.26 | 0.49 | -1.69 | 0.17 | 0.99 |
| PDOlag | 0.20 | 0.37 | -0.50 | 1.03 | 0.69 |
| Group | 0.00 | 0.04 | -0.08 | 0.09 | 0.48 |
| Group\*PDO | 0.01 | 0.05 | -0.05 | 0.16 | 0.26 |
| Group\*PDOlag | 0.00 | 0.05 | -0.11 | 0.10 | 0.15 |
|  |  |  |  |  |  |
| Litter Size |  |  |  |  |  |
| (*Gaussian GLM's*) |  |  |  |  |  |
| Intercept | 3.00 | 0.19 | 2.64 | 3.38 | 1.00 |

**Figure Legends**

Figure 1: Model-averaged probability of breeding as a function of age, previous breeding state, and time. Results are based on 6 years of trapping data (1999-2004) for adult female hoary marmots in the Ruby Range, Yukon. Values are model-averaged annual parameter estimates ± 1 SE.

Figure 2: Apparent survival for adult female hoary marmots in the Ruby Range, Yukon, between 1999 and 2004. Survival probabilities for breeding and non-breeding individuals are shown. Values are model-averaged parameter estimates ± 1 SE.

Figure 3: Change in log-transformed body condition index (mass / zygomatic arch width) over time for non-breeding and breeding female hoary marmots in the Ruby Range, Yukon. Data from 1999-2004 are shown pooled across years. The best fit lines for linear regressions are shown.